Specialized Feeding in Mitrid Gastropods:
Evidence from a Temperate Species,
Mitra idae Melvill

by

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Abstract. The neogastropod *Mitra idae* Melvill is the only member of the family Mitridae on the California coast. Although suspected of being a specialized predator, its food preferences have never been quantified. This study documents the feeding of *M. idae* on sipunculans. Laboratory experiments and gut analysis of field-collected specimens of *M. idae* have revealed that it is a specialized predator preferring the sipunculan *Phascolosoma agassizii* Keferstein.

INTRODUCTION

MEMBERS OF THE gastropod family Mitridae are most common in tropical waters, but some are present in temperate marine waters (CERNOHORSKY, 1970; ABBOTT, 1974; MCLEAN, 1978; KAY, 1979). Although PONDER (1972) has given detailed descriptions of the digestive tract, little is known about the diet. The few species investigated have been shown to prey on sipunculans (KOHN, 1970, 1978; WEST, 1979). Quantitative dietary information is available for only two members of the family, *Mitra litterata* Lamarck, of intertidal beaches in Hawaii, where it specializes on the sipunculan worms, *Phascolosoma* spp. and *Aspidosiphon elegans* Chamisso and Eyserhardt (KOHN, 1970), and *Mitra flavocingulata* of Easter Island, which KOHN (1978) has reported feeding on a species of *Phascolosoma*. TAYLOR (1975) has found juveniles of *Mitra assimilis* in Hawaii to feed on small mollusks under laboratory conditions.

There is some uncertainty as to the number of *Mitra* species occurring along the central California coast. WEST (1979) reports two, *M. idae* and *M. catalinae,* which, he reports, differ in radula structure and proboscis morphology, but which are otherwise alike externally except for size, *M. catalinae* being less than 30 mm in length. However, MCLEAN (1978) considers *M. catalinae* synonymous with *M. idae.* ABBOTT (1974) questioned whether it was a dwarf form of *M. idae,* and MORRIS *et al.* (1980) mention only *M. idae.* If there are two species virtually indistinguishable externally except for size as WEST (1979) has suggested, it means that small animals (<30 mm) may

be either juvenile *M. idae* or *M. catalinae,* and would be indistinguishable without dissection. We were not aware of the potential presence of two species until this study was completed and specimens had been discarded after gut dissection; thus, we were unable to undertake radula and proboscis dissections of small specimens to attempt to verify WEST's (1979) contention. Therefore, those specimens that we have considered here as juvenile *M. idae* (<28 mm) could be a mixture of the two species if WEST's (1979) contention that there are two species is substantiated by other malacologists. In either case, this does not invalidate our main argument of dietary specialization regardless of size. We prefer, pending presentation of more evidence, to follow MCLEAN (1978) and consider all California mitrids as members of one species, *M. idae.*

Mitra idae Melvill is restricted to kelp forests and the low intertidal zone (MCLEAN, 1978; MORRIS *et al.,* 1980). Previous studies of this species have dealt with taxonomy and radular arrangement (CERNOHORSKY, 1966, 1970; COAN, 1966; CATE, 1967), functional morphology (WEST, 1979), and reproductive patterns and behavior (CATE, 1968; CHESS & ROSENTHAL, 1971; KELLOGG & LINDBERG, 1975). Although MORRIS *et al.* (1980) report *M. idae* to be a specialized carnivore, no documentation is provided, nor is the prey identified. Moreover, CATE (1968) was unsuccessful in feeding a variety of potential prey items to *M. idae* in laboratory aquaria. She did not report whether sipunculans were offered to the *M. idae.* WEST (1979), however, has observed *M. idae* to feed upon the sipunculan *Phascolosoma agassizii* and the vermetid gastropod *Petaloconchus montereyensis* in the laboratory. His

accounts represent the most complete descriptions of feeding in the species.

The present study further quantifies the diet of free-living *Mitra idae* and establishes preferences in laboratory experiments. This information should help to establish the role of predation by *M. idae* in the kelp forest and the more general occurrence of sipunculan feeding within the family. Other species and genera remain to be studied to establish a general pattern of specialized feeding on sipunculan worms.

METHODS

The main study area was the kelp forest off Point Cabrillo, Pacific Grove, California (36°37'N; 121°53'W). Additional collection of *Mitra idae* for gut content analyses was done off Del Monte Beach, Pacific Grove (36°37'N; 121°53'W), and Stillwater Cove (36°33'N; 121°56'W) (Figure 1). Descriptions of these kelp forests are given in LOWRY & PEARSE (1973) for Point Cabrillo, in BURNETT (1972) and HOFFMAN (1981) for Del Monte Beach, and in FOSTER (1982) for Stillwater Cove.

All sampling and collecting were done with SCUBA. Estimates of abundance of *M. idae* were made at Point Cabrillo in April and May, 1981. Water depth varied from 5 to 10 m. Random samples were taken along 25-m transects within a 0.25-m² quadrat. All *M. idae* found within these quadrats were counted and measured. Animals used for gut-content analyses were collected haphazardly during day and night, and were boiled shortly after collection to stop further digestion. After recording wet weight and measuring length from the apex of the shell to tip of siphonal canal, each shell was cracked open and the digestive tract dissected. Prey were identified and counted, and state of digestion noted.

Laboratory feeding experiments were conducted to document prey preferences employing two species of sipunculans and other potential prey, and to observe feeding behavior. One sipunculan species, *Phascolosoma agassizii,* was collected from local rocky intertidal areas and the holdfasts of drift kelp. The other sipunculan, *Themiste pyroides* (Chamberlain), was collected from subtidal shale. Prey wet weights were recorded before and after feeding experiments. One set of experiments evaluated the preference of *M. idae* for the two species of sipunculans. In each experiment, one *M. idae* was placed in a dish with one *P. agassizii* and one *T. pyroides*. The experiment was repeated 2–4 times for each *M. idae* used. The dishes were covered with a fine screen to prevent escape and were held in laboratory aquaria with running sea water. Observations continued until one of the prey was consumed or attacked. Sipunculans of similar size were used when possible; however, individuals of *T. pyroides* were generally larger than *P. agassizii*.

In a second set of experiments, each species of prey was presented separately to a specimen of *M. idae*. In addition to the two species of sipunculans, *M. idae* was also pre-
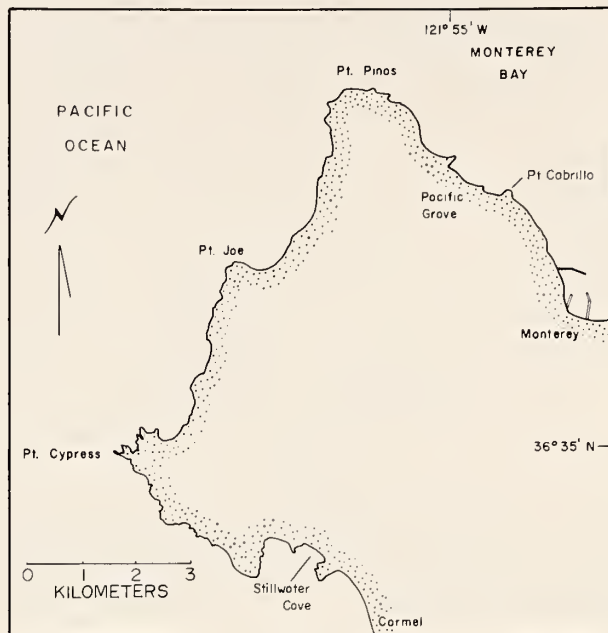

Figure 1

Location of study areas in central California.

sented with the echiuroid worm *Urechis caupo* Fisher and MacGinitie, and the holothuroids *Eupentacta quinquesemita* (Selenka) and *Cucumaria pseudocurata* Deichmann. *Urechis caupo* is a close taxonomic relative of the sipunculans, and the two holothuroids are similar in size and shape to sipunculans.

RESULTS

Individuals of *Mitra idae* were observed subtidally on rock walls, in crevices, in sand pockets, on old holdfasts of the kelp *Macrocystis pyrifera,* under the cover of red algae (*Gigartina* spp. and *Rhodymenia* spp.) and in tube beds of the polychaete *Diopatra ornata* Moore. Although the abundance of *M. idae* was only 0.81/m² (SD = 0.54; n = 106) at Point Cabrillo, individuals were seen in aggregations of up to five individuals. KOHN (1970, 1978) observed 0.05–0.22 *Mitra litterata*/m² in Hawaii and 0.12 *M. flavocingulata*/m² at Easter Island.

Size-frequency plots revealed two distinct size classes at Point Cabrillo, one near 15–20 mm and the other near 40 mm (Figure 2). CHESS & ROSENTHAL (1971) found mean shell lengths for copulating *M. idae* in southern California at 35 mm for males and 51 mm for females. Therefore, the smaller size group (<28 mm) probably was composed mostly of juveniles or a mixture of juveniles and *M. catalinae*.

The gut contents of 41 *M. idae* were examined (Table 1). Three of these individuals were collected at Stillwater Cove, six from Del Monte Beach, and the remaining an-
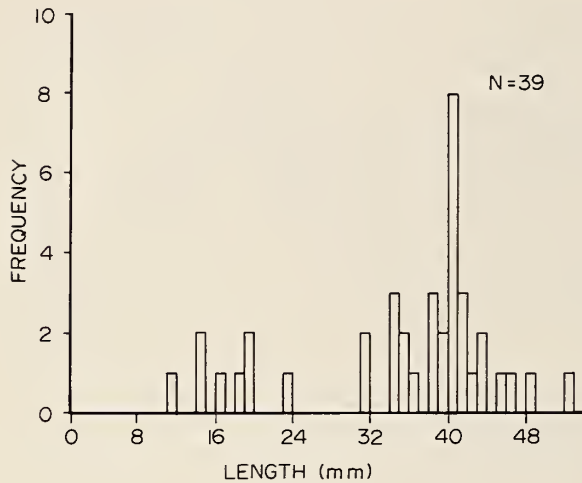
Figure 2

Length-frequency histograms for *Mitra idae* collected at Point Cabrillo. Note the separation of a large ("adult") and small ("juvenile") size class.

imals from Point Cabrillo. Food was found in 22 guts (54%). Sixteen guts contained whole sipunculans or fragments. Five had unidentifiable organic matter, and one gut had the remains of what appeared to be a nemertean worm. The sipunculan was identified as *Phascolosoma agassizii* in 13 of the 16 guts. Only five *M. idae* were collected at night. These were all collected at Point Cabrillo. Two of these individuals had empty guts, two contained fragments of *P. agassizii,* and one had fragments of a nemertean. Most of the 16 juvenile *M. idae* had empty guts; however, one contained part of a *P. agassizii,* and

Table 2

Choice of prey when *Mitra idae* was offered both sipunculans, *Phascolosoma agassizii* and *Themiste pyroides*. *Phascolosoma agassizii* was preferred in every experiment.

	Number of trials	Prey consumed		
Mitra #1	5	*Phascolosoma* (5)	*Themiste*	(0)
Mitra #2	6	*Phascolosoma* (4)	*Themiste*	(0)
Mitra #3	3	*Phascolosoma* (1) *	*Themiste*	(0)
	14	10		0

* *Phascolosoma* attacked but later released (see text).

five others contained unidentifiable organic matter. Among the 25 adults, two contained whole specimens of *P. agassizii* (<0.1 g), and 10 had parts of this species. The sipunculan prey in three adult guts could not be identified to species.

The two-choice feeding experiments indicated that *Mitra idae* has a strong preference for one of the two sipunculan species. *Phascolosoma agassizii* was attacked in 10 of 14 trials. *Themiste pyroides* was not attacked (Table 2). Feeding experiments containing one species of potential prey showed the same pattern. *Phascolosoma agassizii* was consumed in 30 of 45 trials (67%). *Themiste pyroides* was not consumed in any of five exposures to *M. idae* (Table 3). Fewer trials were made with *T. pyroides* because of the longer duration of each experiment. In one experiment, a specimen of *M. idae* was starved for 17 days prior to exposure to a *T. pyroides*. The *T. pyroides* was attacked and held by the proboscis of *M. idae* for over six hours before it was released. However, the *M. idae* did not consume the *T. pyroides*, which suffered no apparent damage

Table 1

Gut contents of *Mitra idae* collected at three areas in central California and in "adult" and "juvenile" sizes from all areas.

	Number of guts examined	Number empty	Number with sipunculans	Amorphous organic matter	Other*
Area					
Stillwater Cove	3	0	0	3	0
Del Monte Beach	6	1	5	0	0
Point Cabrillo	32	18	11	2	1
	41	19	16	5	1
Size of *Mitra idae*					
"Juveniles" <28 mm	16	10	1	5	0
"Adults" ≥28 mm	25	9	15	0	1
	41	19	16	5	1

* Fragment of nemertean worm.

Table 3

Feeding experiments offering *Mitra idae* either one or the other of the sipunculans, *Phascolosoma agassizii* or *Themiste pyroides*. Only *P. agassizii* was consumed.

| Prey species	Number of trials	Total number consumed	Number eaten whole	Pierced and eaten	Attacked, not eaten
Phascolosoma	45	30	25	5	1
Themiste	5	0	0	0	1

Figure 3

The relationship between the size of *Phascolosoma agassizii* and the method of prey consumption. Smaller prey were generally eaten whole and only larger individuals were eaten by puncturing the integument of the prey and inserting the proboscis.

from the attack, and it remained alive in a holding tank. *Mitra idae* neither attacked nor consumed the three sipunculan-like prey, *Urechis caupo, Eupentacta quinquesemita* and *Cucumaria pseudocurata,* in similar feeding experiments.

Laboratory feeding observations indicated two methods of attack and consumption of the *Phascolosoma agassizii.* Prey either were ingested whole or the integument was punctured by the radula and the internal contents removed through the hole, presumably by a mechanism described by WEST (1979). Considering all experiments, 81.5% of the *P. agassizii* were consumed whole (n = 40). Prey weighing less than 0.3 g were always ingested whole, but larger individuals (up to 0.8 g) were taken whole as well. Only seven individuals were eaten by puncturing the integument of the sipunculan. These prey were relatively large compared to those eaten whole, and ranged in size from 0.3 to 0.76 g (Figure 3). The weight loss of pierced prey averaged 64 ± 17% (n = 7) and all pierced animals died.

DISCUSSION

Mitra idae seems to be a specialized carnivore. Although we have tested only one other sipunculan species, gut contents and laboratory feeding experiments indicate that the sipunculan *Phascolosoma agassizii* is the dominant or preferred prey. *Phascolosoma agassizii* is the most abundant sipunculan at all three study areas on the Monterey Peninsula (HOFFMAN, 1981; personal observations). Despite the presence of another sipunculan, *Themiste pyroides,* in the field (HOFFMAN, 1981) and in feeding experiments, this species was not consumed by the gastropod (Tables 2, 3). An echiuran worm and two holothurians also were not eaten in laboratory feeding experiments. Moreover, the guts of *M. idae* collected in the field did not contain any of the abundant polychaete groups that co-occur with *M. idae* (e.g., onuphids, terebellids, sabellids, syllids).

Specialized feeding on sipunculan worms was first established by KOHN (1970, 1978) for the tropical species *Mitra litterata* and *M. flavocingulata.* Now, evidence suggests a similar situation for the temperate species *M. idae.* Although three species is a small sample of the 500 or so
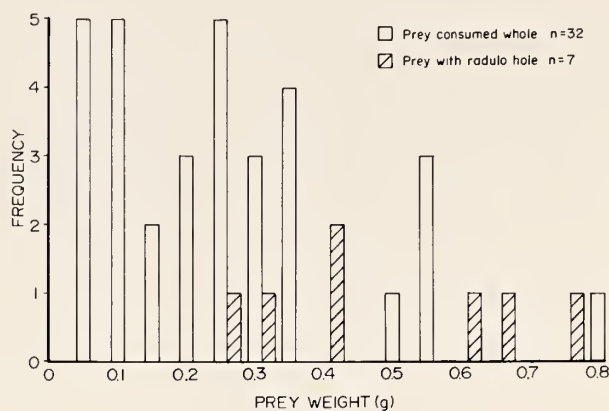
species from this family, the geographical separation of *M. idae* from *M. litterata* and *M. flavocingulata* suggests that a general feeding pattern concentrating on sipunculans may emerge, at least for this genus. Indeed, WEST (1979) has determined that the epi-proboscis of *M. idae* functions to locate, retrieve, and hold soft-bodied prey, in particular, sipunculans. Perhaps sipunculan worms will be the dominant prey for the entire family. Present knowledge does not allow a critical evaluation of this hypothesis, but the distinct morphological similarities in the alimentary canal among members of the family Mitridae reported by PONDER (1972) would argue for this.

Laboratory feeding observations indicated two modes of prey consumption for *Mitra idae.* A few sipunculans were eaten by puncturing the integument, inserting the proboscis, and removing the body contents, as WEST (1979) has described; but most were consumed whole, especially the smaller-sized prey. The proboscis of mitrids may be extended the length of the shell (WILSON & GILLETT, 1972; personal observations). The ability to extend the proboscis a long distance is of practical importance in feeding upon prey that lodge deep in crevices, holdfasts, or other substrata. The two modes of consuming prey also may be of significance in that the extraction of a strongly wedged sipunculan is not necessary. The frequency of puncture feeding is difficult to assess in the field, as empty guts can indicate either the absence of prey or faster digestion of the internal contents of a pierced prey compared to the outer integument of an animal consumed whole.

Gut contents and laboratory experiments suggest that the feeding habits of *Mitra idae* may be more closely related to behavioral preferences and not to prey availability. The ability to survive without food for at least 8–12 months (CATE, 1968; personal observations) supports the

idea that prey availability may not be of critical importance. Size selective predation also may be feasible. Evidence from the few whole sipunculans found in gut contents of *M. idae,* as well as laboratory observations, seem to support this idea. Perhaps future studies will reveal important similarities in the foraging tactics of mitrid gastropods that will allow generalizations to be made about the family. Specialized feeding on sipunculan worms by tropical and a temperate *Mitra* suggests that similar evolutionary processes affected the development of these predator-prey interactions.

ACKNOWLEDGMENTS

LITERATURE CITED

ABBOTT, R. T. 1974. American seashells, 2nd ed. Van Nostrand Reinhold Co. 663 pp.

BURNETT, N. A. 1972. The ecology of the benthic community of bivalve molluscs in the shale at the Monterey sewer outfall. Master's thesis, San Francisco State Univ. 56 pp.

CATE, J. M. 1967. The radulae of nine species of Mitridae. Veliger 10:192–195.

CATE, J. M. 1968. Mating behavior in *Mitra idae* Melvill, 1893. Veliger 10:247–252.

CERNOHORSKY, W. O. 1966. A study of mitrid radulae and a tentative generic arrangement of the family Mitridae (Mollusca: Gastropoda). Veliger 9:101–126.

CERNOHORSKY, W. O. 1970. Systematics of the family Mitridae and Volutomitridae. Bull. Auckl. Inst. Mus. 8:1–190.

CHESS, R. J. & R. J. ROSENTHAL. 1971. On the reproductive biology of *Mitra idae* (Gastropoda: Mitridae). Veliger 14:172–176.

COAN, E. 1966. Nomenclatural units in the gastropod family Mitridae. Veliger 9:127–137.

FOSTER, M. 1982. The regulation of macroalgal associations in kelp forests. *In:* W. Srivastava (ed.), Synthetic and degradative processes in macrophytes. DeGruyter and Co., Berlin. pp. 185–205.

HOFFMAN, R. G. 1981. The ecology of the benthic and endolithic communities of a rocky reef in the kelp beds off Del Monte Beach, Monterey, California. Master's thesis, U.S. Naval Postgraduate School. 117 pp.

KAY, E. A. 1979. Hawaiian marine shells. Reef and shore fauna of Hawaii, Section 4. Mollusca. Bernice P. Bishop Museum Spec. Publ. 64(4). 653 pp.

KELLOGG, M. G. & D. R. LINDBERG. 1975. Notes on the spawning and larval development of *Mitra idae* Melvill (Gastropoda: Mitridae). Veliger 18:166–167.

KOHN, A. J. 1970. Food habits of the gastropod *Mitra litterata* Lamarck: relation to trophic structure of the intertidal marine bench community in Hawaii. Pac. Sci. 24(4):483–486.

KOHN, A. J. 1978. Gastropods as predators and prey at Easter Island. Pac. Sci. 32(1):35–37.

LOWRY, L. W. & J. S. PEARSE. 1973. Abalones and sea urchins in an area inhabited by sea otters. Mar. Biol. 23:213–219.

MCLEAN, J. H. 1978. Marine shells of southern California. Science Series 24, Nat. Hist. Mus. of L.A. County. 104 pp.

MORRIS, R. H., D. P. ABBOTT & E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford Univ. Press, Stanford, Calif. 690 pp.

PONDER, W. F. 1972. The morphology of some mitriform gastropods with special reference to their alimentary and reproductive systems (Neogastropoda). Malacologia 11(2):295–342.

TAYLOR, J. B. 1975. Planktonic prosobranch veligers of Kaneohe Bay. Doctoral thesis, University of Hawaii, Honolulu.

WEST, T. L. 1979. Structure, function, and functional morphology of *Mitra idae* Melvill 1893 and *M. catalinae* Dall 1920. Master's thesis, University of the Pacific. 97 pp.

WILSON, B. R. & K. GILLETT. 1972. Australian shells. Charles Tuttle Co. 168 pp.